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Characterization of the light attenuation by periphyton in lakes of different trophic state

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ABSTRACT

In order to measure the attenuation of light by periphyton a method has been developed which assures that natural periphyton architecture and therefore its optical characteristics remain preserved. This method has been applied to analyze the transmittance of periphyton of four lakes of different tropic states situated in the Osterseen Lake District (Upper Bavaria, Germany). The seasonal variation of the periphyton's transmittance has been studied using standard microscope glass slides exposed 1 m beneath the water surface within macrophyte beds. The study ran from February to November 1997 in two eutrophic lakes (Lake Waschsee, Lake Sengsee) and from May to November 1997 in the meso-oligotrophic Lake Eishaussee and in the oligotrophic Lake Herrensee.

Generally the exposure-period, the seasonality, and the tropic state of the habitat affected the transmittance spectra of the periphyton. In all lakes the attenuation by periphyton increased with longer colonization times but at a different time scale. The periphyton of the nutrient-rich and the nutrient-poor lakes differed clearly in composition and architecture. The eutrophic lakes were characterized by a relatively thick but loosely attached, unstable periphyton community, which was translucent to a certain degree even at the end of the growth period. The transmittance of this periphyton fluctuated considerably and high percentages of filamentous green algae in this periphyton contributed to attenuation maxima within the range 400–500 nm and 650–700 nm due to photosynthetic pigments. By contrast, the periphyton of the meso-oligotrophic and of the oligotrophic lake was quite compact and nearly impervious to light.

Introduction

Nutrient supply and light conditions are the most important factors affecting the occurrence and the distribution of macrophytes. Compared to the large number of publications dealing with nutrient effects (e.g. Carignan and Kalff 1980; Carignan 1985; Chambers et al. 1989; Blindow 1992; Barko and James 1997; Melzer 1999; Rooney et al. 2003; Lacoul and Freedman 2006), relatively few papers have been published on light effects on macrophytes (e.g. Barko et al. 1982; Søndergaard 1988; Sand-Jensen 1990; Middelboe and Markager 1994; Krause-Jensen and Sand-Jensen 1998; Binzer and Sand-Jensen 2002). Three primary factors control the light conditions of macrophytes: (1) the light regime above the water surface, which depends on the season and the adjacent terrestrial features, (2) the light attenuation by phytoplankton, inorganic particles, and dissolved substances in the overlaying water column, and (3) the shading by periphyton. The attenuation of light caused by periphyton is an issue addressed only in a few publications (e.g. Sand-Jensen 1977; Phillips et al. 1978; Sand-Jensen and Søndergaard 1981; Meulemans 1987; Sand-Jensen 1990, Sand-Jensen and Borum 1991; Van Dijk 1993; Strand and Weisner 1996).

Sand-Jensen and Søndergaard (1981) described a method to determinate the attenuation of the periphyton. They recommend to scrape the periphyton from the substrate and to emulsify this material with water. The attenuation of the light passing through this emulsion was determined with a quantum sensor and corrected for the sampling area of the substrate. Subsequently a different approach, described by Van Dijk (1993), used intact periphyton films that grew on glass slides. The colonized slides were analyzed in a glass beaker filled with water with the quantum sensor placed directly under the beaker. These methods did not allow for the fact that a part of the light passing though the periphyton is scattered. There are only a few previous studies that actually considered the light attenuation of periphyton. In these cases the undisturbed periphyton complex was measured with a spectral photometer with an integrating sphere, as we have done in this study as well (James et al. 2000; Roberts et al. 2003). During the last decade numerous investigations focused on shallow eutrophic lakes which exhibit alternative stable states

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(ASS) (e.g. Körner 2001; Blindow et al. 2002; Jeppesen et al. 2003; Irfanullah and Moss 2004; Jeppesen et al. 2007). Within distinct limits of nutrient concentrations the dominance of either phytoplankton and turbidity or macrophytes and clear water occur alternatively. The presence or the absence of macrophytes is controlled by the underwater light climate which, among other things, depends on phytoplankton abundance. Additionally, Roberts et al. (2003) discussed the shading of macrophytes by periphyton in a eutrophic shallow lake to explain ASS. However, the impact of periphyton on the light climate of macrophytes in lakes of different trophic state is almost unexplained, despite the early study of Sand-Jensen and Søndergaard (1981). As a first important step to close this gap we studied the attenuation of periphyton of oligotrophic, mesotrophic and eutrophic lakes. Future studies about the impact of shading by periphyton on the occurrence and distribution of different macrophyte species are necessary; therefore methodological details are given.

Study area

The Osterseen Lake District developed after the last glacial period and is situated south of Lake Starnberg in Upper Bavaria, Germany (Fig. 1). The system consists of 20 small lakes connected by natural channels. The lake system is almost exclusively fed by ground water with a small contribution from one tributary. Originally, all lakes of the Osterseen Lake District were oligotrophic – hardwater lakes – but from their genesis to now they developed differently. On the one hand all the lakes exhibit approximately the same morphology and are exposed to the same climatic environmental factors. On the other hand ground water input and anthropogenic pollution of the lakes vary extremely. Therefore, within a small area, a broad spectrum of different lakes regarding their hydrological and chemical conditions can be found. Each selected lake represents a different trophic state (Table 1): Lake Waschsee (eutrophic), Lake Sengsee (mesotrophic), Lake Eishaussee (mesotrophic) and Lake Herrensee (oligotrophic).

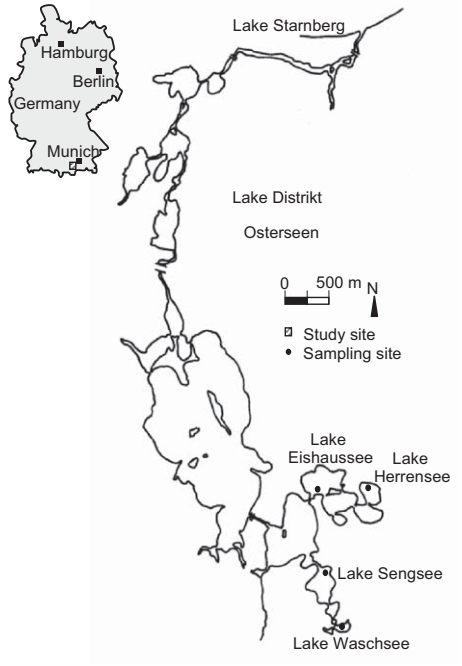

Fig. 1. Map of the study site. The experiments were conducted in Lake Waschsee, Lake Sengsee, Lake Eishausee and Lake Herrensee.

Materials and methods

Exposure of substrate

To study light attenuation by periphyton, standard microscope glass slides (76 mm × 26 mm) were exposed for different time periods in the selected lakes (Fig. 1). Special racks (Fig. 2) were constructed by acrylic glass square bars (Sahlberg, Germany, 1-component-polymerisaton-adhesive, Acrifix 192, Röhm, Germany). Onto each rack 10 glass slides were fixed with waterproof, ecologically compatible silicon adhesive (Rhône-Poulenc Silicon GmbH, France). Ten racks were positioned at 1 m depth in the lake by fixing them with polyamide cords (∅ 5 mm) on a wooden frame (0.5 m × 3.0 m, Fig. 2). Depending on the experiments each frame was equipped with 6–10 racks. Two spans filled with ready-mixed concrete anchored the frame with PVC ropes (∅ 12 mm) about 50 mm below the water surface. This was necessary to prevent birds from sitting on the frame and hence changing nutrient conditions for periphyton by excrements. The extensive influx of groundwater with a constant temperature of 8–10 °C into Lake Waschsee and Lake Sengsee keeps these lakes nearly ice-free. Therefore we started the exposition of substrate in these eutrophic lakes already in February. Due to ice-cover the experiments in Lake Eishaussee and in Lake Herrensee could not be started until May.

Sampling

Every month one new rack with new slides was exposed and two racks with coated slides were sampled. One rack had been exposed for 1 month (colonization 1 month = C1) and one rack that had been exposed from the beginning of the experiment (colonization × month = CX, Table 2). In order to measure its transmittance, completely undisturbed periphyton architecture has to be assured. To prevent losses or damages to the periphyton the acrylic glass rack was hoisted to approximately 0.3 m beneath the water surface and put into a plastic tray. This water-filled container was lifted into the boat. To avoid aeration of periphyton ten colonized glass slides were transferred underwater each into an Erlenmeyer flask. Due to its form only the flange of the glass slides contacted the wall of the Erlenmeyer flasks. Subsequently samples were stored cool and dark until measurement.

Experimental design

The light transmittance of the periphyton-coated slides was measured with a double-beam spectrophotometer (Hitachi 150-20) equipped with an integrating sphere, a so-called Ulbricht-sphere. It enables the analysis of the spectral transmittance of diffuse scattering samples. The Ulbricht-sphere consists of a hollow ball with a highly reflective coating inside. Small openings on the two opposite sides of the sphere are provided for the probing of the sample in transmittance and reflection mode, respectively. By comparing the intensity of the light entering the sphere through the sample side beam path and the reference side beam path, the built-in photo detector determines the absorption coefficient of the sample.

Samples were measured in custom-made composite cuvettes fixed on a special cell holder (Fig. 3). Two glass slides, a clamping device and a U-shaped rubber gasket constituted the cuvette. The growth of one side of the glass slide was removed completely with a razor blade. Thereafter the glass slide was fixed in the clamping device with the intact periphyton directed towards the inner side of the cell. The other wall of the composite cell was comprised of an unused glass slide. A reference cuvette was assembled in

Table 1
Characteristics of Lake Waschsee, Lake Sengsee, Lake Eishaussee and Lake Herrensee.

Lake	Lake Waschsee	Lake Sengsee	Lake Eishaussee	Lake Herrensee
Volume ($\times 10^3$ m^3)	26	388	495	155
Area (ha)	0.9	5.5	7.7	3.0
Perimeter (km)	0.4	1.0	1.3	0.7
Maximum depth (m)	4.5	15.2	19.1	10.7
Mean Secchi depth (m)	3.2	3.8	5.4	5.2
Mean total phosphorus at depth of 1 m (μg l^{-1})	51.9	25.7	11.8	7,6
Stratification type	Dimictic/Holomictic	Dimictic/Holomictic	Dimictic/Meromictic	Dimictic/Holomictic
Trophic state	Eutrophic	Eutrophic	Oligo-mesotrophic	Oligotrophic

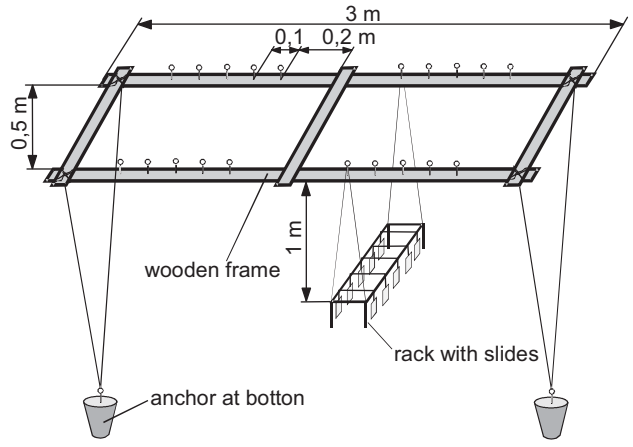

Fig. 2. Construction and components of the racks for the exposition of glass slides in macrophyte beds as substrate for periphyton.

Table 2
Time schedule for the colonization of glass slides 1 m beneath the water surface in Lake Waschsee, Lake Sengsee, Lake Eishaussee and Lake Herrensee.

Sampling month	Colonisation time (month)							
	Waschsee		Sengsee		Eishaussee		Herrensee	
	C1	CX	C1	CX	C1	CX	C1	CX
March	1		1					
April	1	2	1	2				
May	1	3	1	3				
June	1	4	1	4	1		1	
July	1	5	1	5	1	2	1	2
August	1	6	1	6	1	3	1	3
September	1	7	1	7	1	4	1	4
October	1	8	1	8	1	5	1	5
November	1	9	1	9	1	6	1	6

exactly the same manner with two clean slides. Thereafter the composite cuvettes were filled with temperate deaerated water in order to avoid vesication. Finally, the transmittance spectra of periphyton were measured from 300 nm (ultraviolet) to 850 nm (weak infrared) in 10 nm band increments. According to DEV (2008) a statistically reliable procedure was developed to validate the results of the measurement. This is warranted in case of measuring six selected points (Fig. 3) of five covered slides. That means 30 measurements for each sample.

Results

All results of the 4-week and the long-term experiments are summarized in Fig. 4. Every spectrum shows that the

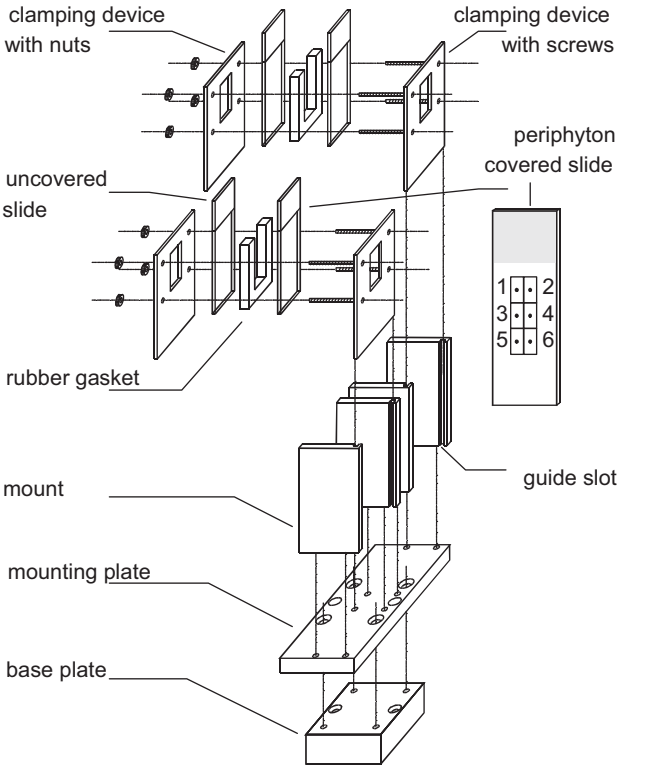

Fig. 3. Construction and components of the custom-made composite cuvette to measure periphyton transmission with a double-beam spectrophotometer.

transmittance of the periphyton varies depending on the wavelength. Generally the transmittance of periphyton increased from 300 to 850 nm. In the majority of cases the transmittance of periphyton decreased in the range 650–700 nm. This decrease was most distinctive in the eutrophic Lake Waschsee and apparent in the eutrophic Lake Sengsee. The periphyton samples from the meso-oligotrophic Lake Eishaussee and the oligotrophic Lake Herrensee also showed a reduction of their transmittance in the range of 650–700 nm, but this was pronounced only slightly. Another decrease of the periphyton's transmittance was observed in the range 400–500 nm in the eutrophic lakes, especially in Lake Waschsee; however, this was less significant than the decrease between 650 and 700 nm.

Generally the periphyton of the 4-week experiments (C1) exhibited higher transmittance than the periphyton of the long-term experiment (CX) of the same lake. The only exceptions were the transmittance spectra of periphyton of Lake Waschsee in June (C4) and in August (C6). In June the light attenuation of the periphyton form the 4-week experiment exceeded those from the long-term experiment. In August the results of both experiments were almost identical. After every 4 weeks (C1) in Lake Waschsee

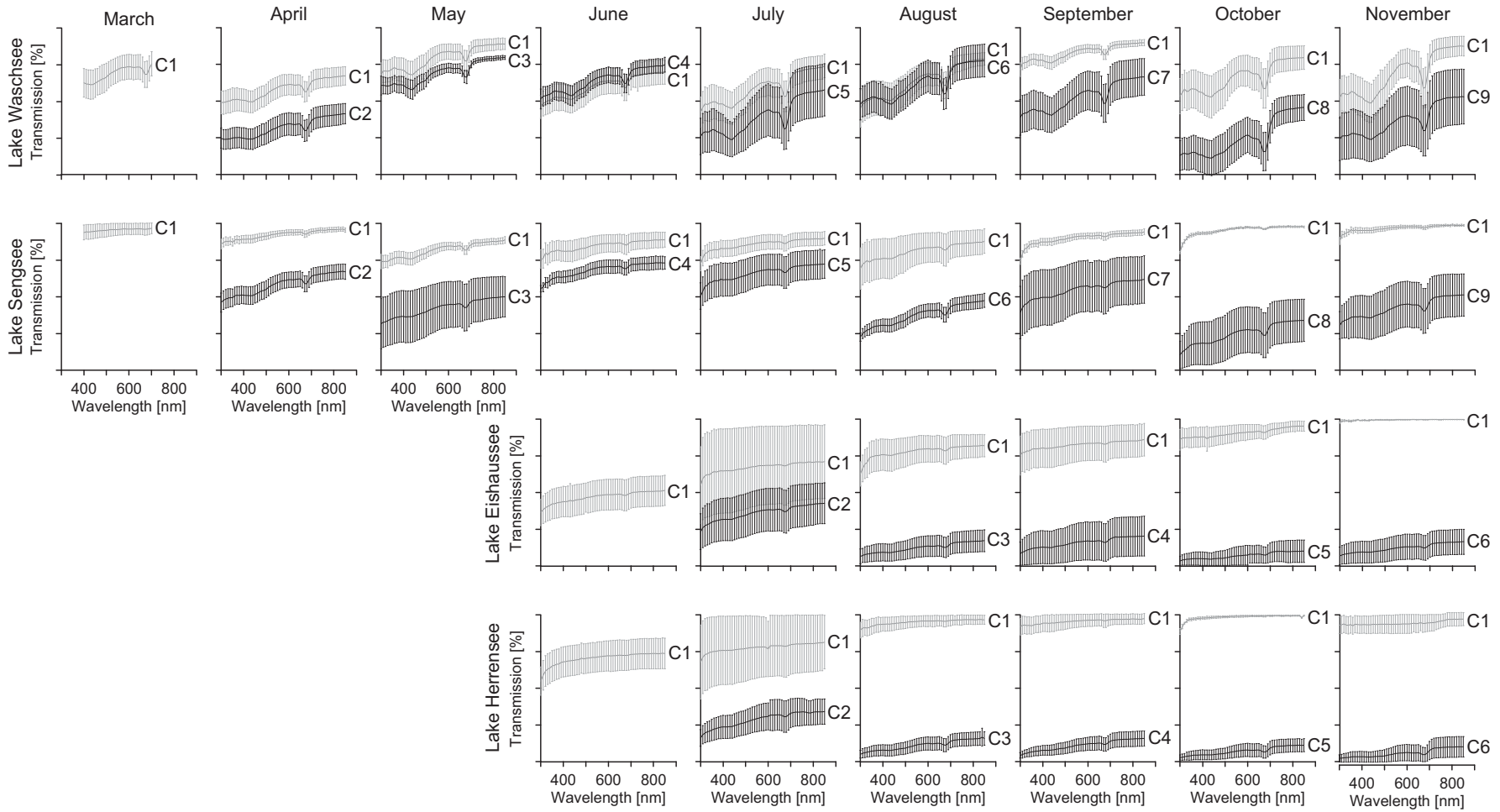

Fig. 4. Seasonality of transmittance spectra of periphyton from 300 to 800 nm (mean ± standard deviation, $n = 30$) in each 10 nm band depending on the time of colonization ▒▒▒; C1 = colonization 1 month; ▒▒▒; CX colonization × month, from the beginning of the experiment.

the thickness of the periphyton film on the slides was similar and created the same spectral light attenuation. The transmittance of the periphyton amounted to about 50% in the ultraviolet range to 75% in the red band. Only in May and in September a lower light attenuation by 4-week-old periphyton films was observed. In Lake Waschsee the transmittance of the periphyton of the long-term experiment (CX) fluctuated until June. Thereafter the periphyton covering of the slides increased until the end of the study and the light attenuation by periphyton increased correspondingly. In October (C8) in Lake Waschsee periphyton was characterized by its transmittance minimum with 13% (300 nm) to 46% (850 nm).

In Lake Sengsee the periphyton films that developed within 4 weeks (C1) were thinner than in Lake Waschsee, in particular in October and in November. Consequently in Lake Sengsee the periphyton films of the 4-week experiment were characterized by higher transmittance, especially at the end of the investigation period. From May to August transmittance of periphyton ranged approximately from 75% (300 nm) to 90% (850 nm). In Lake Sengsee the long-term experiment (CX) showed that the transmittance of the periphyton decreased from April (C2) to May (C3). Surprisingly the slides which had been exposed for 4 months from February to June (C4) had less periphyton cover, and accordingly the transmittance of the periphyton was greater. Subsequently the periphyton films on the exposed slides became denser and the transmittance decreased until the end of the experiment. The lowest transmittance of periphyton was detected in October (C8) when transmittance of the periphyton amounted to 11% (300 nm) and to 34% (850 nm).

Within meso-oligotrophic Lake Eishaussee and oligotrophic Lake Herrensee a solid periphyton film, which reduced transmittance significantly, developed during the 4-week experiment (C1) in May and in June. Within the entire study the highest light attenuation by 4-week-old periphyton was observed in Lake Eishaussee in June, when transmittance declined to 36% in the range of ultraviolet to 51% in the red band. In Lake Eishaussee the periphyton film which grew in August and in September reduced the transmittance on average to 75%. A very thin periphyton layer on the exposed slides minimized their transmittance in October and November in Lake Eishaussee, and from August to November in Lake Herrensee.

In the long-term experiment (CX) in meso-oligotrophic Lake Eishaussee and in the oligotrophic Lake Herrensee the slides were heavily overgrown after 2 months. In July (C2) in Lake Eishaussee the transmittance of the periphyton was reduced by 23% (300 nm) to 43% (850 nm), in Lake Herrensee we detected only 16% transmittance in the range of ultraviolet to 34% in the red band. In both lakes the periphyton layer on the slides became cumulatively more solid over the months. The slides which were exposed until November (C6) were covered with abundant periphyton (Fig. 5). Consequently the transmittance of the overgrown slides decreased drastically. In October (C5) the transmittance of the periphyton was reduced to its minimum (3% at 300 nm–10% at 850 nm) in Lake Eishaussee, and only 3% (300 nm) to 11% (850 nm) in Lake Herrensee.

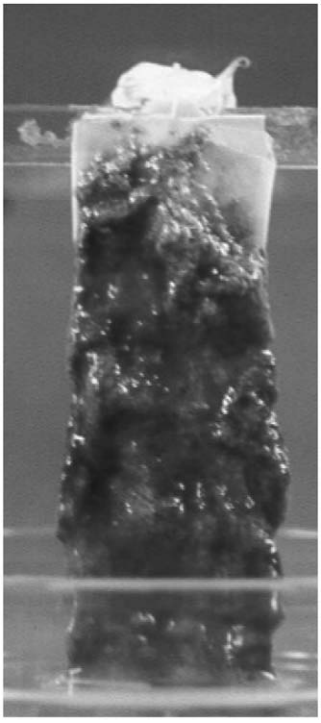

Fig. 5. Periphyton on a glass slide exposed 1 m beneath the water surface form May to October (colonization time 5 month = C5) in the oligotrophic Lake Herrensee.

Discussion

According to the definition of Wetzel (2001) the term periphyton describes a complex community composed of algae, bacteria, fungi, animal inorganic matter and organic detritus that is attached to every underwater substratum. In general periphyton develops in the following stages. The colonization of the substrate begins with bacteria that segregate a thin layer of bacterial extracellular polymeric substances (EPS). This conditioning of the substrate surface is important for further colonization (Zobell and Allen 1935; Skerman 1956; Allen 1971 all cited in Hamilton and Duthie 1984). Hamilton and Duthie (1984) assume that this primary biofilm provides a local nutrient cycle that facilitates colonization by algae. According to this model the epiphytes incorporate the nutrients released by the biofilm immediately so that the nutrients will not be flushed away (nutrient spiraling). In contrast to this Hoagland et al. (1982) consider that the layer of EPS is important for mechanical reasons because it promotes the attachment of algae. These two models are not mutually exclusive and we believe that both are important.

The constituents of the EPS are polysaccharides, proteins (e.g. exoenzymes), and glycoproteins. The structure of the EPS is amorphous and highly aqueous. The organisms (bacteria, algae, fungi) grow within the biofilm and consolidate it to a compact periphyton. In addition, filiform bacteria, filamentous and stalked diatoms, filamentous fungi and green algae expand from the biofilm and extend into the ambient water. Inorganic and organic particles from the overlaying water column continuously trickle into this periphyton matrix and will be embedded into the periphyton film. These deposits derive from living organisms and organic detritus as well as inorganic components like lime, sediment, and frustules of dead diatoms (Wetzel 2001). All these components generate an attenuation of light passing through an intact periphyton layer.

The results of this study confirm clearly the attenuation of light by periphyton in eutrophic and also in oligotrophic lakes. In all cases the transmittance spectra of the periphyton run approximately parallel to each other and increased with ascending wavelength. Our results indicate an unspecific light attenuation at all wavelengths. The different components of the periphyton lead to a decline of transmittance within the range of photosynthetic active radiation in a similar manner (Meulemans 1987; Kirk 1994). The results of the 4-week experiments (C1) revealed that light attenuation caused by periphyton changes seasonally.

This effect is considerably more pronounced in the meso-oligotrophic Eishaussee and in the oligotrophic Herrensee than in the eutrophic lakes, Lake Waschsee and Lake Sengsee.

A distinctive light attenuation by periphyton occurred between 650 and 700 nm, and was less prominent between 400 and 500 nm. These maxima of attenuation rely on the photosynthetic pigments of the periphyton, especially on living diatoms and on green algae. The non-specific chlorophyll *a* and also the specific chlorophyll *b* and chlorophyll *c* feature absorption maxima between 630 and 665 nm as well as between 430 and 455 nm. In addition accessory photosynthetic pigments such as carotenoids absorb between 400 and 500 nm (Yentsch et al. 1980; Antoine and Benson-Evans 1983; Kuehl and Jøregensen 1994).

The attenuation by photosynthetic pigments was observed after a colonization time of only 4 weeks (C1) in the eutrophic lakes, especially in Lake Waschsee but also in Lake Sengsee. During longer colonization times (CX) the noticed absorption maxima intensified in the nutrient-rich lakes. In these lakes a rapid growth of periphyton was observed. This was characterized by chain-forming diatoms and high percentage of filamentous green algae, mainly *Cladophora*, *Ulothrix*, *Spirogyra* and *Oedogonium*, (unpublished data) that caused the "fluffy" appearance of the periphyton. This finding coincides with the results of Cattaneo (1987). She observed that the algae fraction of periphyton in oligotrophic lakes was almost exclusively dominated by diatoms. With increasing phosphate concentration the percentage of total algae biomass in periphyton rose due to the development of filamentous green algae. The loosely attached algae of the eutrophic lakes became very thick but unstable and gradually reduced the transmittance of periphyton within the long-term experiment (CX). The literature often noted the phenomenon of autogenic sloughing when slides were exposed for several months (CX), especially in eutrophic lakes. This is due to the die-off of the algae of the lower layers and the increasing weight of the periphyton (Sand-Jensen and Søndergaard 1981; Meulemans and Roos 1985; Cattaneo 1987; Meulemans 1987; Morgenroth and Wilderer 2000; Boulêtreau et al. 2006). These detachment processes might have been responsible for the fluctuations that were observed in the periphyton's transmittances of the eutrophic lakes. In Lake Waschsee the transmittance of 1-month-old periphyton (C1) was somewhat lower than the transmittance of 4-month-old periphyton (C4). The result might be interpreted with the phenomenon of sloughing as well.

In the less eutrophic lakes, the absorption by photosynthetic pigments also was observed but apparent only in some month-old periphyton (CX). In total the contribution of algae to periphyton was lower, and was attributed to diatoms only (unpublished data). In the nutrient-poor lakes, the architecture of periphyton was quite different to that in the eutrophic lakes. In Lake Eishaussee and in Lake Herrensee the cubic dimension of the periphyton was small, but it was compact and very close-packed. Virtually no sloughing was observed within the duration of the study. Therefore a solid periphyton with a high amount of inorganic components was established and persisted until November (unpublished data). Van Dijk (1993) also observed that the periphyton accrual rates were highest in the beginning of summer. This corresponds to an increase in water temperature and photon flux density. In our study, the periphyton layers attenuated more than 80% of the light already after 3 months (C3). At the end of our experiment the periphyton of the nutrient-poor lakes did not penetrate light.

Light conditions in the overlaying water column and grazers in the periphyton film control the development of periphyton in different ways, and much work has been devoted to describe these strong linkages (e.g. Bourassa and Cattaneo 2000; James et al. 2000; Rosemond et al. 2000; Liboriussen et al. 2005; Hillebrand 2008). We regard the structure of periphyton, developed in the macrophyte beds of the selected lakes, as the overall result of the interacting factors at their natural sites. Due to the climatic conditions the long-term experiment lasted 9 months in the eutrophic lakes, Lake Waschsee (C9) and Lake Sengsee (C9), and 6 months in the meso-oligotrophic Eishaussee (C6) and in the oligotrophic lake Herrensee (C6). Despite shorter exposition times, the attenuation of the solid and compressed periphyton of the nutrient-poor lakes was significantly greater than the attenuation of thicker but loosely attached periphyton of the nutrient-rich lakes.

In general, the light conditions for macrophytes are impacted by the light regime above the water surface, the light attenuation in the overlaying water column, and the shading by periphyton. The presented study contributes to the understanding of the shading effects by periphyton in lakes of different trophic state. In addition, the methods used in this study provide an appropriate tool to measure the light attenuation due to periphyton.

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